LIFE HISTORY OF SHOOTS OF
CAREX COMOSA F. BOOTT.

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ABSTRACT

Carex comosa shoots have a life history which varies depending on their time of emergence. Shoots that emerge in spring, summer or early autumn develop flower initials before winter, flower the following year, then die in August, having lived 240–420 days. Shoots that emerge in late autumn do not develop flower initials, remain vegetative the next summer, then develop flower initials in the second autumn. These shoots flower and die the following summer, having lived for up to 700 days. Few shoots live their maximum time and mortality is 90% in some cohorts. Mortality patterns indicate that shoots die at a constant rate throughout the year.

Key Words: *Carex*, life history, ramets, central New York

INTRODUCTION

Many temperate zone wetland ecosystems are dominated by clonal *Carex* plants. Such plants (genets) are capable of producing large numbers of shoots (ramets) through continuous reiteration of modules. Each shoot is typically separated by a spacer organ, usually a rhizome.

Different clonal sedge species have evolved different life history adaptations. Bernard (1990), in his review of *Carex*, noted three basic patterns of growth based on behavior of the spacer organ. He pointed out that some species have spacers which are short, resulting in tight clumps of shoots, while others have long rhizomes and place shoots at a distance from the parent shoot. The third and probably most common type is found in those shoots that produce both long and short rhizomes, resulting in loose clumps of shoots connected to other loose clumps through the rhizomes.

There has been a relatively large number of studies on *Carex* species exhibiting the latter two strategies, among them those by Bernard (1975, 1976), Bernard and Gorham (1978), Bernard and MacDonald (1974), Callaghan (1976, 1990), Costello (1936) and Ratliff (1983) but few on those that produce only short spacers and grow in clumps. Examples are the studies of David and Kelcey (1985) on the *C. muricata* L. complex, Schmid (1984) on *C. flava*

L., Taylor (1956) on *C. flacca* Schreber, and Bernard and Fiala (1986) on *C. comosa* Boott.

Carex comosa is a large clump-forming species whose shoots produce short rhizomes only. It is found scattered in disturbed areas of wetlands. Bernard and Fiala (1986) found that the smallest clones were made up only of vegetative shoots, but as the clones grew larger the flowering percentage increased to a maximum of almost 70% in the largest 100-shoot clones. The shoot/root ratio also increased as the clones expanded in size. From their study, they labelled *C. comosa* a long-lived fugitive species which invades gaps in wetlands, grows vegetatively for the first years, then flowers heavily when larger. This adaptation enables *C. comosa* to invade a gap, increase in ramet numbers and hold the gap for a decade or more while producing large crops of seeds, some of which may find new gaps to invade.

The purpose of this study was to determine life history and demographic patterns in shoots of *Carex comosa* and to determine if there are phenological differences in plants growing in different sites.

METHODS

Data were collected from three different study areas, two in the Cumming Nature Center, Naples, New York and one in Inlet Valley, Ithaca, New York. The Inlet site was the same one used by Bernard and Fiala (1986) and was dominated by *Sparganium eurycarpum* Engelm. Botanical nomenclature follows Gleason and Cronquist (1991). A small stream flowed through the site with a row of willows (*Salix* sp. L.) bordering one side. One of the Nature Center sites was just downstream from an active beaver (*Castor canadensis*) dam. The water table was just at the surface of the soil during the growing season; the vegetation was a mixture of many species including *Typha latifolia* L., *Carex lacustris* Willd. and *Leersia oryzoides* (L.) Swartz. There was a considerable number of trees at the site and tree branches were common on the ground. The second Nature Center site was upstream from the beaver dam along the pond shore. This site had less herbaceous cover with a few scattered alders (*Alnus incana* L. Moench.). The water table was somewhat lower and the organic soil more consolidated than at the site below the dam.

All shoots of *Carex comosa* in the 14 clones growing in the two

sites at Cumming Nature Center were tagged with a numbered plastic tag in the autumn of 1983 or spring of 1984. The length of all shoots/clone were measured then and at subsequent visits at approximately monthly intervals during the growing season until autumn 1985. All shoots tagged on each date became part of a cohort. Notes on the health of shoots and whether they were in vegetative or flowering condition were made at each visit. New shoots were tagged as they emerged. In order to determine if differences in mean number of shoots per plant above and below the beaver dam at the Nature Center were significant, a sample *t*-test was conducted.

In a separate part of the study, all shoots in three clones were tagged on November 5, 1983 in Inlet Valley. There were 64 shoots in the three clones varying in length from 3.5 cm to over 100 cm. All shoots were placed in four cohorts, defined differently than those above; cohort 1 was made up of the smallest shoots which had just emerged above ground plus four additional shoots that emerged after November 5. Cohorts 2 and 3 were shoots which had emerged in summer and early autumn and grew to heights of 10–20 cm by November. Cohort 4 was made up of shoots over 30 cm long; most had a cluster of dead leaves at the shoot bases. These clones were visited four times between November 5 and June 22, 1984. At each visit, other non-tagged clones were harvested. These were brought back to the laboratory, individual shoots measured, then dissected to determine if the shoots had flowering initials present. All shoots were dried and weighed after dissection.

RESULTS

Table 1 presents data on the total number of shoots in each of nine clones located at Site 1 at the Nature Center, downstream from the beaver dam. Shoot numbers in five of the clones increased from 80 to 400%, one clone remained the same, and three declined over the 25-month period of study. The total number of shoots in all clones went from 77 to 134 after one year, then increased slightly to 139 after the second year, for a total gain of 80%. Shoot number during both summers increased about 35% but varied dramatically during the two winter periods. From September 1983 to May 1984, shoot numbers increased 28%, but from September 1984 to May 1985, they decreased by 22%. Thus,

Table 1. Number of shoots/clone and total numbers in nine clones of *Carex comosa* sampled over a two-year period. The site was located in a wetland just downstream from a beaver dam (Site 1).

Clone	1983 9/19	1984 5/21	1984 9/17	1985 5/24	1985 10/17	9/83–10/85 % Change
1	5	10	13	17	25	400
2	7	15	15	10	25	257
3	8	10	17	16	19	137
4	15	13	28	21	28	87
5	15	20	29	22	27	80
6	4	7	10	5	4	0
7	9	9	8	6	7	−22
8	6	7	9	4	2	−66
9	8	7	5	3	2	−75
Totals	77	98	134	104	139	81%

although the average shoot percentage gain was 80% over two years, almost all the gain was during the first year; little change occurred during the second year. It is important to note that four of the clones were probably dying, two having two shoots remaining, and two having the same number or fewer shoots than at the beginning of the study.

Table 2 presents data for five clones growing at Site 2 along the edge of the pond upstream from the beaver dam. All clones increased at least 220% in total shoot numbers from May 1984 to October 1985, the average being 445%. Although mortality in winter was 18%, almost the same as clones at Site 1, emergence in summer was heavy; clones gained 152% from May to October 1985, a rate similar to the 164% growth of the previous summer.

Table 2. Number of shoots/clone and total numbers in five clones of *Carex comosa* at Site 2, located along the edge of a beaver pond.

Clone	1984 5/21	1984 9/17	1985 5/12	1985 10/17	5/84–10/85 % Change
1	5	20	16	57	1040
2	5	19	16	29	500
3	6	10	13	34	466
4	6	13	11	20	233
5	9	20	11	29	222
Totals	31	82	67	169	445%

Table 3. Cumulative gains and losses and percentage change of *Carex comosa* shoots in nine clones at Site 1 and five clones at Site 2. Note: births and deaths are cumulative for each period; for example, between 5/21/84 and 7/3/84, 34 new shoots emerged and 12 died.

	Site 1				Site 2			
Date	Births	Deaths	Total Shoots	% Turn-over	Births	Deaths	Total Shoots	% Change
9-19-83			77					
5-21-84	36	15	98	20			31	
7-3-84	70	27	120	18	9	1	39	25
7-30-84	86	52	111	−8	18	3	46	18
8-21-84	127	77	127	14	51	6	76	65
9-17-84	160	103	134	6	65	14	82	7
5-24-85	186	159	104	−22	80	44	67	−18
6-24-85	202	163	116	12	136	55	112	67
7-23-85	252	170	159	37	159	66	124	10
8-26-85	286	211	152	−4	229	88	172	38
10-17-85	339	277	139	−9	308	170	169	−1

In comparison to Site 1 clones, the number of shoots in all Site 2 clones had at least doubled and one had increased over 10 times.

Shoot turnover for both sites is shown in Table 3 which gives the cumulative gains and losses during the sampling period. At Site 1, from September 1983 to October 1985, the total shoots increased from 77 to 139 but a total of 339 new shoots had emerged and 277 had died. At Site 2, total shoot numbers were 31 in May 1984 and increased to 169 in October 1985. Again, significant shoot turnover occurred with 308 shoots emerging and 170 dying.

Shoot mortality during the two winter periods varied during the study. During the first winter at Site 1, only 15 shoots died but 36 new shoots emerged, resulting in a 20% increase. In contrast, during the second winter, plants had high mortality with relatively low emergence resulting in a total loss of 22% of all shoots in the nine clones.

Clone numbers at Site 2 (Table 3) showed a somewhat different picture. Plant mortality over winter was high (54%), but emergence during the following spring was somewhat higher, resulting in a decline of 18% in total shoot numbers over winter.

Figure 1 shows the time of emergence for all cohorts of shoots in nine clones making up the population at Site 1 on July 23,
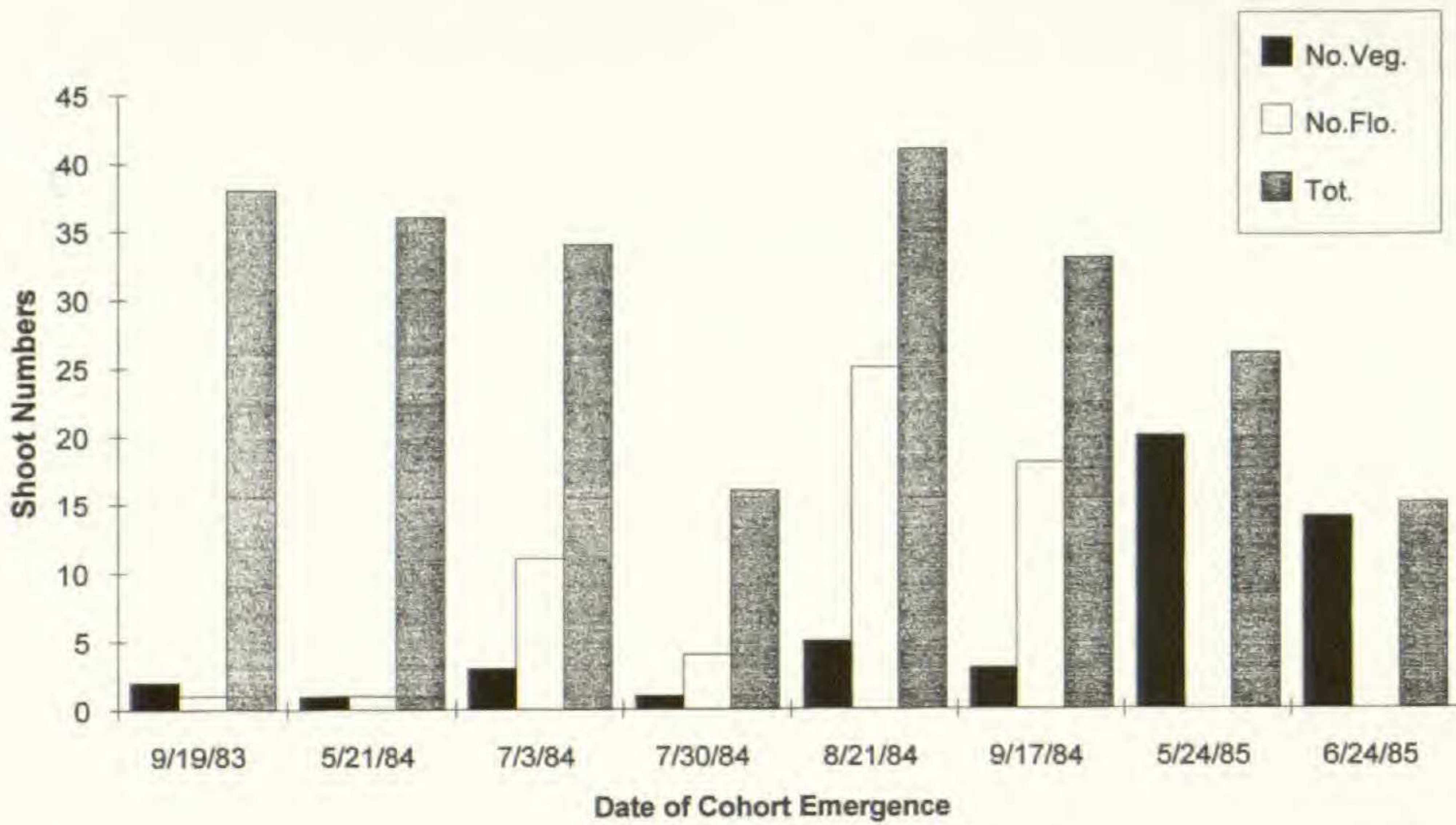
Figure 1.   Age structure of 109 shoots in nine clones of *Carex comosa* on July 23, 1985. The total number of shoots originally tagged (shaded bars) in each of the dated cohorts is shown as is the number of vegetative (black bars) and flowering (open bars) shoots still alive.

1985. Bars represent the original number of shoots in each cohort (shaded) and the number of vegetative (black) and flowering shoots (open) still remaining at the end of the study. The oldest cohorts (9/1/83, 5/21/84, 7/3/84, 7/30/84) had very high mortality; few
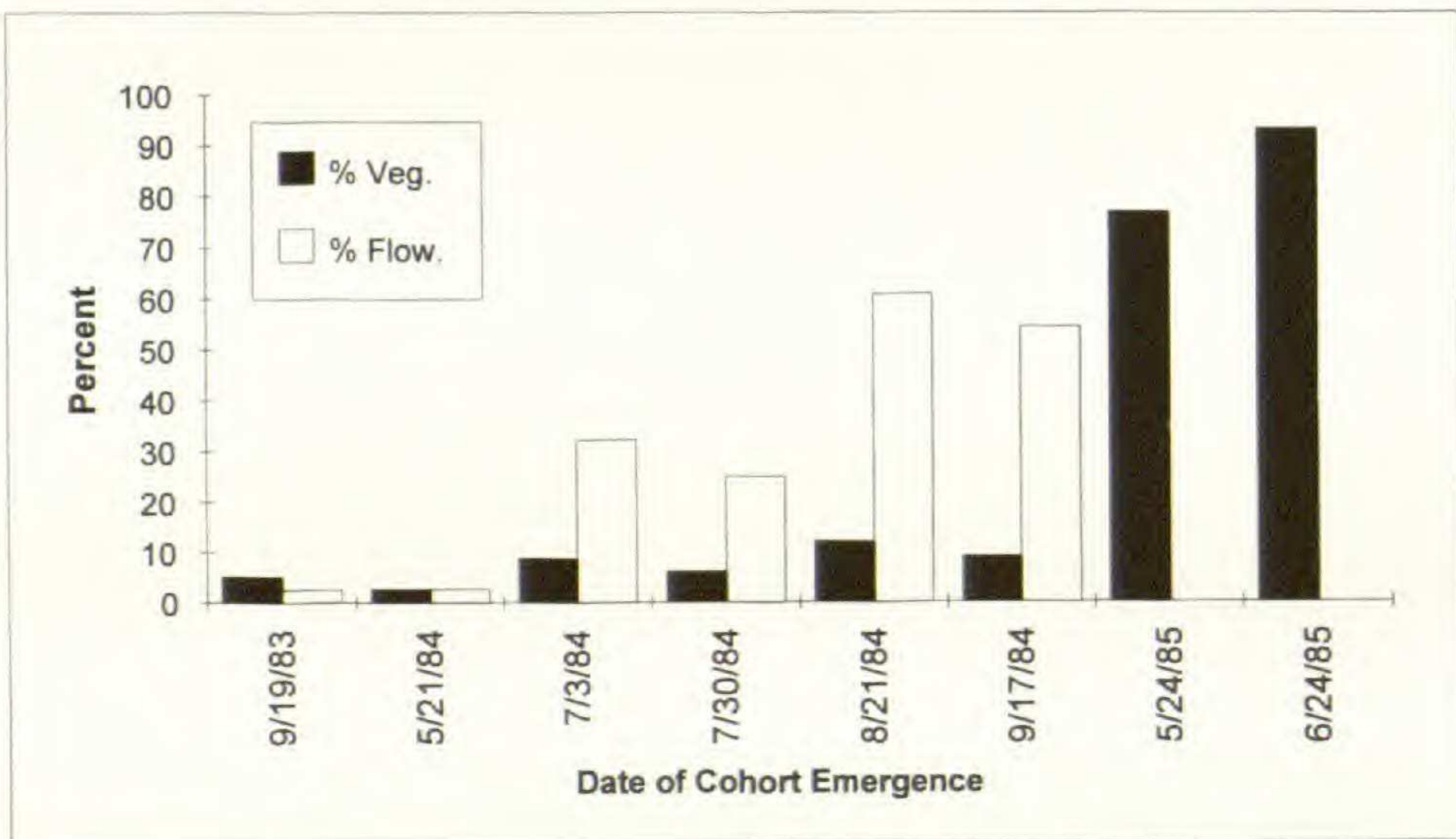

Figure 2.   Percentage of vegetative (black bars) and flowering shoots (open bars) of *Carex comosa* remaining on July 23, 1985 from original number in the cohorts.

Table 4. Number of shoots in four cohorts of overwintering clones of *Carex comosa* at the Inlet Valley site.

Cohort	1984	1985		
	1/15	3/10	4/29	6/22
1	11	15	15	14*
2	25	26	26	26*
3	15	15	15	15*
4	13	13	12	6*
Totals	64	69	68	61

* Denotes shoots in flower.

shoots remained from the original number that had emerged. Mortality was less in the second 1984 cohort, and most that lived, flowered. None of the 1985 shoot cohorts flowered. Figure 2 gives percentages of vegetative and flowering shoots in the eight cohorts still living on July 23, 1985. The two oldest cohorts of autumn 1983 and May 1984 had over 90% shoot mortality; about half the survivors flowered. The rest of the 1984 cohorts had higher percentages living and most were flowering shoots. The youngest shoots of the 1985 cohorts were all vegetative and although having emerged only 1–2 months before July had considerable mortality, the June cohort having a 7% mortality.

Recently emerged shoots were all vegetative, but older cohorts, with the exception of the September 1983 cohort, had mostly flowering shoots. At the conclusion of the study, two shoots two years old were still in a vegetative condition, and 55% of shoots in all clones had flowered. Mortality patterns described a type II survivorship curve, a pattern to be expected of an opportunistic early successional species (Deevey, 1947).

In a separate part of the study, three clones were tagged in late autumn in the Inlet Valley site near Ithaca and followed during the winter and early spring. There were 64 shoots in the three clones tagged in November (Table 4); four additional shoots emerged in cohort 1 by March 10 and one additional larger shoot was tagged and placed in cohort 2. Of the total 69 shoots, 61 survived until June 22, with one shoot in cohort 1 and six of the original 13 in cohort 4 dying. The shoots that survived until June in all four cohorts averaged about 102 cm in length and all flowered.

In addition to the shoots placed in the four cohorts, almost all shoots in cohorts 2 and 3 produced one or more small axillary

shoots, all less than 3 cm long in March; at harvest in June these axillary shoots accounted for the largest percentage of vegetative shoots in each clone since none flowered. Cohort 1 and cohort 4 shoots did not produce any axillary shoots over winter during this study. We found that 37 of the 107 shoots harvested (35%) produced axillary shoots after November 5, a percentage about twice that of shoots in cohorts 2 and 3 of the tagged clones. Some of the harvested shoots which were old enough to have produced axillary shoots did not. These were all either smaller than average size, had brown meristems, or were infected with *Diptera* larvae.

DISCUSSION

Maximum length of life for single shoots of various *Carex* species is extremely variable. Some, such as *Carex lacustris*, live 12 months (Bernard, 1975); others such as *C. rostrata* may live for about 18–24 months in the temperate zone (Bernard, 1976) but longer, up to 60 months, in oligotrophic sites in northern Sweden (Solander, 1983). Many arctic and alpine tundra species also live for up to 60 months (Alexeev, 1988; Hultgren, 1988), as do some montane species. A particularly good example of long-lived shoots was found in *C. nebraskensis* Dewey, some of which lived for 96 months in alpine habitats of the Sierra Nevada Mountains in California (Ratliff, 1983).

Few *Carex* shoots live their maximum possible time and annual mortality is usually at least 80% in temperate sites although lower in arctic sites. Life spans are variable even in shoots in the same cohort, ranging, for example, from only 12 days to over 750 days in *C. lasiocarpa* Ehrh. (Bedford et al., 1988). Bedford et al. (1988) found, as did we, that shoots die at a constant rate, a situation also shown in other studies of *Carex* (Bernard, 1990). Shoots that emerge in late autumn or early winter have the longest possible life span in comparison to spring or summer emerged shoots but these differences are not as different as they at first appear. If one subtracts the approximately 140 days of winter from the autumn-emerged shoots the average life span becomes less variable. For example, shoots emerging in late autumn live for 670–700 days or so, the longest of all possible life spans, while spring shoots live for perhaps 550 days. Subtracting the 140 days of winter from the autumn shoots gives them approximately the same life span as spring shoots. It is the same situation described by Bedford et

al. (1988), who noted that both autumn and spring emerged shoots of *C. lasiocarpa* were part of the same cohort, the shoots not emerging until spring were already formed but were dormant below ground during the winter.

There is extremely heavy shoot turnover depending in part on whether or not individual clumps grew well. This has also been found in other *Carex* species. Bartlett and Noble (1985), Noble et al. (1979), Bernard (1990) and Callaghan (1976) all noted that at a time of favorable growth conditions, more shoots are produced than are needed for replacement; when the environment worsens, they die back. Thus, the better the environment for growth, the more emergence. When conditions become less suitable, greater than average mortality occurs. This mortality does not happen in more northern sites; Solander (1982) found little mortality in *C. rostrata* in her arctic study, owing probably to the low nutrient status of her site.

Mortality patterns did not match well in the years of study. During the first winter, clones showed low shoot mortality at both Nature Center sites but during the second winter clones had very high mortality, especially at Site 1. This may have been due to a high water table at Site 1 during the second winter; the water table at Site 2 did not vary to the same extent. The high second-year mortality at Site 1 had a profound effect on individual clones, some of which did not recover.

Flowering percentages in clumps varied for two reasons. First, size of clumps was important. Bernard and Fiala (1986) found that shoots in the smallest (and probably youngest) clones did not flower while the largest clones had as many as 67% of their shoots in flower. Second, we found in this study that during winter vegetative meristems of some shoots were either dead or affected by *Diptera* larva. These conditions obviously affect expected flowering percentages.

Bernard and Fiala (1986) noted that *Carex comosa* had the characteristics of an opportunistic early successional species, invading open sites, growing rapidly and then flowering. It also had characteristics that allowed it to live for a long time in a site favorable for growth. The shoot life history patterns found in this study allow this species to both compete for favorable sites while at the same time producing flowering shoots which will distribute seed each year. Thus, while larger clones produce many flowering shoots, there are always vegetative shoots and short rhizomes

present to carry on the genet in autumn after flowering shoots die.

SUMMARY AND CONCLUSIONS

Carex comosa shoots may live for up to 700 days, those emerging in autumn usually being longer-lived than shoots emerging in spring and summer. Shoots that emerge in summer and early autumn will develop flower initials during autumn and flower the next June. These flowering shoots also develop axillary shoots during late autumn and early spring which grow and provide a population of young vegetative shoots during the summer. These emergence and growth patterns ensure that mature clones are always a mixture of flowering and vegetative shoots, the former for producing seed to be disseminated to new sites, the latter to provide the clone with a young shoot population after death of the flowering shoots in August. This is important because *C. comosa* acts as a fugitive species, only occupying a site for a certain time so seed production is essential to its establishment in new disturbed sites (Bernard and Fiala, 1986). Other species which grow by both long and short rhizomes may dominate an area; they tend to flower much less and instead reproduce mostly by vegetative means.

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